The reproductive ecology of exotic Trachemys scripta elegans in an invaded area of southern Europe

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ABSTRACT

1. The main reproductive parameters of exotic Trachemys scripta elegans in established populations from two ponds in southern Spain are described.

2. Females were found to reproduce at 5 years of age, although sexually mature individuals of 4 and 3 years of age were also detected. Annual reproductive frequency was estimated to be 80–86% of reproductive females. Mean clutch size was 11.5 eggs and was not correlated with maternal body size.

3. The number of follicles of different size in ovaries suggested that four or more clutches could be laid per season. Eggs were laid from April to June (inclusive) mainly during morning hours, when females were easily detected during nesting trips. 79.5% of eggs were fertile.

4. Reproductive parameters of this species in southern Spain were of similar or even higher values than in native areas, thus placing them among chelonian species of earlier maturity.

5. Although chelonians might never be considered explosive breeders, the number of T. s. elegans individuals could surpass that of native aquatic chelonians in southern Spain, where T. s. elegans reach maturity earlier, are more fecund and their eggs are more fertile.

KEY WORDS: exotic turtles; reproduction; life history traits; population establishment

INTRODUCTION

The introduction of exotic species poses a serious threat to aquatic ecosystems. Trachemys scripta elegans, an intentionally introduced species, is considered to be among the most common reptile pets traded worldwide (Salzberg, 1995, 1998; Lowe et al., 2000; Telecky, 2001; Reed and Gibbons, 2003). In recent decades millions of hatchlings of this species, a popular pet, have been exported from USA farms to many countries. Nowadays, free-living individuals are reported in countries on the five continents of the world (Newberry, 1984; Gasperetti et al., 1993; Luiselli et al., 1997; Chen and Lue, 1998; Brinjsøe, 2001; Cadi et al., 2004; Feldman, 2007; Perry et al., 2007). While in some countries successful reproduction is considered unviable (e.g. in New Zealand: Feldman, 2007), in many others, such as Mediterranean countries, these turtles find favourable conditions for field incubation of eggs. Successful reproduction has been reported in several countries outside of

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its native range, such as in France (Cadi et al., 2004), Italy (Ferri and Soccini, 2003), Taiwan (Chen and Lue, 1998), and in a wide number of localities within Spain (Brinjsøe, 2001; Pleguezuelos, 2004). Frequent release of pet turtles by their owners coupled with their considerable reproductive output favour the establishment of naturalized populations. However, established populations in countries where they are non-native have only been reported in Taiwan (Chen and Lue, 1998), the Caribbean islands (Perry et al., 2007) and in Spain (Perez-Santigosa et al., 2006a), although the actual distribution of reproductive populations has not previously been studied in detail.

In Spain, the introduction of exotic turtles is considered to threaten the status of the two native species of aquatic turtles (Emys orbicularis and Mauremys leprosa), which are at present listed as vulnerable, with declining populations (Pleguezuelos et al., 2004). Recent studies have demonstrated the influence of competition of this species with the European pond turtle Emys orbicularis, the most widely distributed aquatic chelonian in Europe, at present considered to be a threatened species (Cadi and Joly, 2003, 2004). In Spain, free-living individuals of T. s. elegans were first reported in 1996 (Garcıa-Parıs and Martın, 1997), and the species now occurs throughout the country, including the Canary and Balearic Islands (Pleguezuelos, 2004).

This paper is based on the analyses of exotic turtles removed from two established populations in southern Spain. The aim of this study was to describe their main reproductive characteristics, information basic to the analysis of population trends and demography, to enable a comparison with the dynamics of native turtle species. Reproductive parameters, such as age at maturity and fecundity, may be used to evaluate the ability of turtles to establish wild populations in natural habitats. Other detailed information, such as the description of the nesting season, may be of special interest for improving programmes to eradicate these exotic turtles.

METHODS

This study was carried out in two coastal lagoons, El Acebuche and El Portil (in the province of Huelva, south-western Spain). Wild populations of T. s. elegans have established themselves in these lagoons after successful reproduction of pet turtles released by owners around 1996–1998. A detailed description of these populations was reported in Perez-Santigosa et al. (2006a).

From 2002–2006, a programme for removing exotic turtles was carried out in both localities. More than 250 adult turtles were removed from El Acebuche and 400 from El Portil. A sample of 100 females from El Acebuche and 99 females from El Portil were included in this study. From 2002–2004, 53 females were captured by hand while migrating for nesting, and 60 females and juveniles were trapped with baited submerged traps. In 2005, 86 turtles were captured with basking traps, which notably increased the efficiency of exotic turtle trapping (Perez-Santigosa et al., 2006b). The hour (in GMT) at which nesting females were found was recorded. All individuals were euthanized with thiopental sodium injection (Tiobarbital, Braun Medical), and their straight carapace length (SCL) and plastron length (PL) were measured with callipers (± 1 mm), and body mass (± 1 g) was recorded with an electronic balance. The ovaries and oviducts from 34 females from El Acebuche and 31 from El Portil were extracted, weighed and preserved for later examination. Body mass of females with shelled eggs in oviducts was recalculated by subtracting clutch mass.

After a preliminary inspection of external characters of individuals, they were classified as juveniles or adults. Dissected young females with ovaries with developing follicles, eggs, or distended oviducts indicative of recent oviposition were considered adults. Shelled eggs borne in females were counted and their length, width and mass measured. Clutch mass was estimated as the sum of masses of all eggs, and relative clutch mass (RCM) was calculated as the ratio of clutch mass to body mass of females. Follicles in oviducts were classified in four groups, according to diameter (I) <7 mm (their number were not included in results), (II) 7–13 mm, (III) 14–20 mm; (IV) >21 mm; following Moll and Legler (1971). The number of clutches that females lay per season was estimated from the number of follicles of various sizes and eggs (after Moll and Legler, 1971). Age of individuals was estimated by skeletochronology, counting the number of annuli in an 18 m section of the femur, after tinction with haematoxylin (see details of this technique in Castanet and Smirina (1990)). Total number of annuli was considered equivalent to the age of females. Annual frequency of reproduction was estimated from data on females captured with aquatic traps in 2004 (18 in El Acebuche, and 21 in El Portil), not from data on nesting females, as the latter data could have led to an overestimation of frequency.

Females captured in 2004 and 2005 were inspected by inguinal palpation to detect oviductal eggs and seven gravid females from El Acebuche and two from El Portil were induced to oviposit by injection of oxytocin (Ewert and Legler, 1978). Eggs were also obtained from 14 nests (of recent oviposition) from El Portil and two from El Acebuche. In order to estimate the proportion of fertile eggs, 227 eggs from 25 different clutches were incubated in moistened vermiculite at a constant temperature of 28.5°C. These eggs, used in different experiments, were not uniformly subject to identical moisture conditions, and so the values obtained for

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hatching rate were not included in this study. Fertility rate was estimated as the number of eggs which hatched or contained embryos as a proportion of the total number of incubated eggs. All those eggs which did not hatch were opened and inspected to determine the presence or absence of embryos.

Comparison of variables from females, eggs and hatchlings of the two study sites were tested with ANOVA, using locality as a grouping factor. ANOVA with month as a grouping factor was also used to analyse ovarian mass variation, including data from all dissected females from both localities. The relationship among clutch size and SCL of females was analysed with Pearson correlation coefficients. The description of the main reproductive characteristics is indicated by mean ± standard deviation (sd).

RESULTS

Body size and age at maturity

Adult females from both localities did not differ in SCL, PL and body mass (Table 1). The youngest adult female was 3 years old, although only 32% of females of this age appeared sexually mature, with mature ovaries. Also 64% of 4-year-olds and 92% of 5-year-old females were mature, as were all older females. Eggs or recent oviposition were only detected in females 5 years or older. Because these are young populations, no individual older than 13 years was captured during the study period (Figure 1). The smallest adult female was 170.7 mm SCL (Table 1), while the smallest egg-bearing female was 184.9 mm SCL, 179 mm PL and 864 g.

Reproductive frequency

Considering only those dissected females not captured in their nesting migrations, 12 out of 15 (80%) females captured in El Acebuche had enlarged or preovulatory follicles, eggs or distended oviducts, suggesting recent oviposition. The remaining three females did not show signs of oviposition nor follicle development, although they were sexually mature. In El Portil lagoon, 18 out of 21 females examined (85.7%) showed signs of reproduction.

The annual reproductive cycle

Ovaries differed significantly in mass among individuals captured in different months ($F_{6,51}$=0.587, P=0.0001). Females with heaviest ovaries were found in April, and a gradual decrease of ovarian mass was recorded in the following months until July. In those months most females had follicles of the three largest size-classes, and eggs (Table 2). Lowest ovarian masses were recorded during summer months (July–September), when a period of quiescence is considered to occur, as reported for Trachemys venusta from Panama (Moll

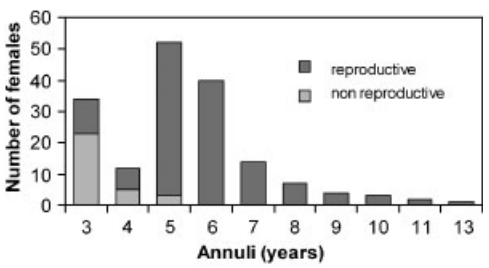

Figure 1. Age estimated by annuli counted in sections of humeri in adult and subadult female Trachemys scripta elegans.

Table 1. Mean, standard deviation and range (min-max) of straight carapace length (SCL), plastron length (PL) and body mass (excluding clutch mass) of females; clutch size, length, width and mass of eggs; relative clutch mass (RCM=clutch mass/body mass); and straight carapace length, plastron length and mass of hatchlings. Results of ANOVA between values of the two populations studied are also indicated.

	Acebuche				Portil				ANOVA
	n	$\bar{x}$	std dev	min-max	n	$\bar{x}$	std dev	min-max	
Female SCL (mm)	99	212.06	15.87	170.7–257.8	95	209.90	18.48	171.0–248.3	$F_{1,192}$=0.765, P=0.383
Female PL (mm)	99	201.06	14.42	159.5–236.0	95	196.59	17.19	159.5–232.1	$F_{1,192}$=3.851, P=0.051
Female mass (without eggs) (g)	100	1419.50	321.00	718.0–2700.0	96	1397.26	356.58	797.0–2204.0	$F_{1,194}$=0.211, P=0.647
Clutch size (eggs)	29	11.34	2.45	6–15	22	11.73	2.07	9–16	$F_{1,49}$=0.338, P=0.563
Egg length (mm)	26	33.48	2.03	29.45–39.10	20	34.12	3.02	28.26–39.53	$F_{1,44}$=0.732, P=0.397
Egg width (mm)	26	21.81	0.82	20.35–23.47	20	21.89	1.39	18.80–24.87	$F_{1,44}$=0.056, P=0.815
Egg mass (g)	26	9.43	1.14	6.88–11.80	20	9.74	1.85	7.04–14.32	$F_{1,44}$=0.463, P=0.500
RCM (%)	25	7.15	1.70	3.85–10.10	20	7.30	1.99	3.91–11.31	$F_{1,42}$=0.052, P=0.821
Hatchling SCL (mm)	8	28.383	1.82	24.35–30.55	10	29.16	1.75	26.47–31.60	$F_{1,16}$=0.851, P=0.370
Hatchling PL (mm)	8	27.15	2.15	22.0–28.5	10	26.92	2.01	24.25–29.79	$F_{1,16}$=0.056, P=0.816
Hatchling mass (g)	8	6.71	0.98	4.50–7.48	10	6.81	1.21	4.88–8.64	$F_{1,16}$=0.034, P=0.856

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Table 2. Monthly variation of the percentage of females with follicles of different size groups, or with oviductal eggs; and of the mean number and range of follicles or eggs

Month	n		Class II	Class III	Class IV	Eggs
April	6	% females	100	100	83.3	66.7
		mean number of follicles	16.2 (15–19)	23.5 (12–41)	10.0/11.8(5–19)	11.0 (8–13)
May	11	% females	90.9	100.0	18.2	54.6
		mean number of follicles	15.5 (12–22)	25.8 (12–42)	3.9/17.0 (15–19)	11.8 (10–13)
June	11	% females	81.8	100.0	36.4	90.9
		mean number of follicles	11.8 (11–23)	18.3 (10–24)	5.5/13.5 (5–17)	11.4 (9–14)
July	18	% females	77.8	55.6	5.6	50.0
		mean number of follicles	15.1(11–51)	16.8 (7–26)	0.5/7.0 (7–7)	11.0 (8–15)
August	11	% females	100	18.2	0	0
		mean number of follicles	25.5 (7–46)	25.5 (15–36)	0	0
September	4	% females	75.0	25.0	0	0
		mean number of follicles	37 (35–39)	8.0	0	0
November	2	% females	100	100	0	0
		mean number of follicles	47.5 (42–53)	16.0 (11–21)	0	0

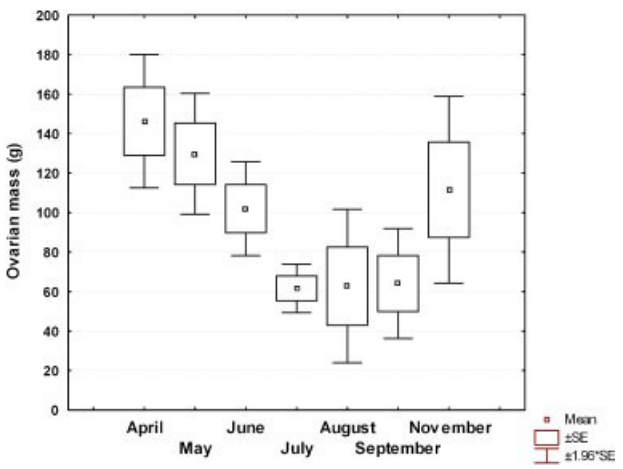

Figure 2. Monthly variation in mass of ovarian follicles measured in female Trachemys scripta elegans from established wild population in southern Spain.

and Legler, 1971). The oviposition period was April–July. From August–September, females did not bear eggs, nor large follicles (class IV), but mainly contained small follicles (Class II); a small proportion of females also contained a small number of preovulatory follicles (Class III). In November, an increase in mass of the ovaries was detected, corresponding to the phase of follicle enlargement, just before the winter inactivity period when all females had follicles of Class I and II only (Figure 2, Table 2).

Clutch number

Because a wide variation in the number of Class II follicles was recorded every month, even after the oviposition period had finished, it was assumed that these follicles were not necessarily related to clutches produced in the current year, but might correspond to clutches of the following year. Thus, as only a proportion of follicles in class III and all of class IV are involved in annual fecundity, the number of clutches was approximated by the sum of the number of Class III and IV follicles and of eggs divided by the number of oviductal eggs of the last clutch when detected (or by mean clutch size, when females had already oviposited). In April and May, females seemed to bear at least three clutches, with eggs and follicles of Groups III and IV. The large number of enlarged follicles in group III and IV of some females suggests that they could lay four or even more clutches per year (Table 2).

Clutch size and egg characteristics

Mean clutch size was 11.5 ± 2.31 eggs, and did not differ between both localities ($F_{1,49}$=0.338, P=0.563) nor among the different months of the nesting season ($F_{3,43}$=1.450, P=0.242). The lowest mean value of clutch size was found in April and the largest in May (Figure 3). SCL and body mass of females were not correlated with clutch size (SCL: r=0.113, P=0.432; Body mass: r=0.046, P=0.751). Average values of egg length, width and mass are given in Table 1, using all values obtained from nests and oviducts, as significant differences among measurements were not observed for eggs obtained with different techniques. These egg variables did not differ between females from both localities (Table 1), and neither did they differ in relation to clutch size. Clutch mass constituted on average $7.2 \pm 1.8\%$ of female mass, and RCM did not differ between localities (Table 1).

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Hatchlings

Mean values of SCL, PL and body mass of hatchlings are shown in Table 1. These values corresponded to individuals hatched from eggs incubated in the laboratory, and were not significantly different from eggs from both localities. However, data recorded from six hatchlings from two nests naturally incubated in the field did not reveal differences in mass (mean=7.11 ± 2.36 g), but they had longer SCL (mean=32.24 ± 3.20 mm, $F_{1,18}$=5.98, P=0.025) and PL (mean=30.91 ± 2.70, $F_{1,18}$=6.41, P=0.021) than hatchlings from laboratory-incubated eggs. These differences may be explained because individuals were measured in the laboratory immediately after hatching, when their shell could still be curved due to their position inside the egg, while hatchlings incubated in the field but not yet emerged from the nest were extracted from the nest approximately 1 month after hatching. Hatchling SCL and mass were not correlated with maternal characteristics, but they were positively correlated with egg length ($r_{egg\ length \times hatchling\ mass}$ ¼ 0:591; P=0.008; $r_{egg\ length \times hatchling\ length}$ ¼ 0:593; P=0.007) and mass ($r_{egg\ mass \times hatchling\ mass}$ ¼ 0:607; P=0.006; $r_{egg\ mass \times hatchling\ length}$ ¼ 0:458; P=0.048).

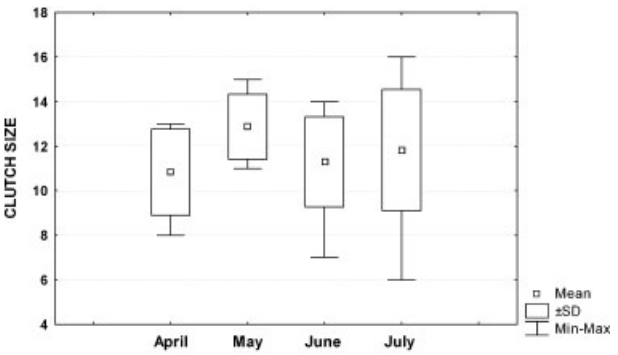

Figure 3. Clutch size of female turtles captured in different months of the nesting season.

Nesting

Females were found migrating for nesting or coming back to the lagoon from early April to 23 July. Except for one female, which was found nesting in the evening in June (17:00), all females nested from 7:30 to 14:00 (Figure 4). However, a variation in the time at which females nested was observed among the different months of the nesting season ($F_{3,26}$=3.182, P=0.041). In April females were found nesting from 09:30 to 14:30, while later in the season nesting was

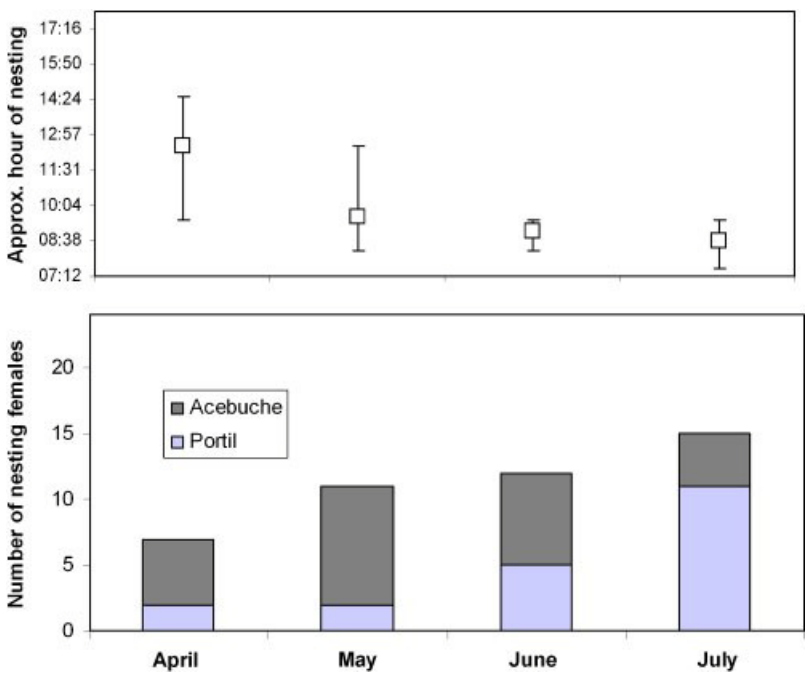

Figure 4. Number of Trachemys scripta elegans females captured on land in their nesting migrations, and monthly variation of the mean (maximum and minimum) hour at which females were found nesting throughout the nesting season. An exceptional female nesting at 17 h in June is not shown.

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mainly concentrated earlier in the morning, before the warmest periods of the day in summer months (Figure 4).

Egg fertility

On average, 79.5% of the eggs of each clutch were fertile, with no significant differences between localities ($F_{1,23}$=0.001, p=0.997). All eggs (100%) were fertile in 50% of the clutches obtained from El Acebuche and 33.3% from El Portil. The minimum fertility rate corresponded to one clutch from El Acebuche, in which only one of the three eggs incubated was fertile.

DISCUSSION

Female size and age at maturity

Several studies have analysed the size and age of sexual maturity in female Trachemys in North America, where a wide variation is observed among populations, species and subspecies (Cagle, 1950; Moll and Legler, 1971; Gibbons et al., 1981, 1982; Gibbons and Greene, 1990; Mitchell and Pague, 1990; Moll and Moll, 1990; Vogt, 1990; Close and Seigel, 1997; Tucker and Warner, 1999; Aresco, 2004).

In Trachemys scripta, sexual maturity is influenced mainly by body size rather than age of females (Cagle, 1950; Moll, 1979; Wilbur and Morin, 1988; Gibbons and Greene, 1990). Females mature with a plastron length of 160–170 mm, and observed differences in growth rate imply differences in the age of sexual maturity. Thus, in very productive habitats, turtles reached mature size at a younger age (4 years old, Congdon and Gibbons, 1983) than in other localities, where females matured at 6–8 years old (Congdon and Gibbons, 1983; Gibbons et al., 1981; Frazer et al., 1990; Mitchell and Prague, 1990). These data correspond to the subspecies T. s. scripta, while for the subspecies T. s. elegans, there is no precise information about the age and size at maturity, although reproductive females were reported from 167 mm PL (Tucker and Moll, 1997).

The data from the present study showed that, as an exotic invader, T. s. elegans in southern Spain may reach maturity at 159.5 mm PL and at 3 years old, although at this age only a small percentage of females were mature, while most 5-year-old females were mature. This early maturity suggests that in these localities, exotic turtles have a similar, or an even higher, growth rate than in the most productive habitats of the native range of the species. The delayed age of maturity of chelonian species, attributable mainly to a greater investment in survival than in reproduction (Congdon and Gibbons, 1990; Iverson, 1992), is characteristic of a life-history strategy with low reproductive rates and low population increase (Wilbur and Morin, 1988; Congdon and Gibbons, 1990). The earlier maturity ages of female T. s. elegans, although detrimental to adult longevity, may benefit the initial establishment of these exotic species populations, as it reduces the time elapsed before incorporation of new individuals. In fact, the time required for establishment of these populations in the wild is at least 3–4 years, the minimum time that the first individuals born in the wild need to become reproductive. Compared with other species of chelonians, maturing from 4 to 25 years of age (see review in Iverson, 1992), T. s. elegans females in southern Spain reach maturity at a notably early age.

Reproductive frequency

Turtles are considered organisms of moderate investment in reproduction (Wilbur and Morin, 1988; Congdon and Gibbons, 1990), and females of many species do not reproduce every year (see references in Frazer et al., 1990). In their original range, 50–70% of female T. scripta reproduce annually in some localities (Congdon and Tinkle, 1982), and 27.2–47.1% in others (Cagle, 1950; Gibbons and Greene, 1990). In contrast, in southern Spain the reproductive frequency of exotic female T. scripta was notably larger (80–85% reproductive females per year), thus increasing the reproductive potential of newly established populations relative to populations in their original range. This difference may be due to the younger age of females in the exotic populations studied. Wild populations in North America are composed of individuals of a wider age structure, and it is probable that reproductive frequency may be affected by the age of females, or even by senescence of older individuals (Frazer et al., 1990). In fact, the oldest female captured in Spain was 13 years old, while in native US populations, females are reported to reach at least 31 years (Frazer et al., 1990).

Nesting period and clutch number

North American female T. scripta nest from mid-April to early August (Cagle, 1950; Congdon and Gibbons, 1983; Jackson, 1988; Aresco, 2004), although the subspecies T. s. elegans is reported to nest only in May and June (Aresco, 2004). In the present study area, the nesting period of this exotic species was 4 months, similar to the longer period in the original range of T. scripta. This long period is favoured by the climatic character of the study area, in which other reptiles such as the terrestrial chelonian Testudo graeca (Dıaz-Paniagua et al., 1996) have a similar nesting season. In contrast, the two native aquatic turtles of the same study area concentrate their nesting in only two months, mainly June and July (Keller and Busack, 2001; Roques et al., 2006).

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In North America, females mainly nest on warm days after rains. In southern Spain, a gradual increase in temperature and notable decrease in rainfall occurs throughout the nesting period, so that the last two months are dry and hot. A similar 4 month nesting period was reported for these exotic aquatic turtles in France, although delayed to May–August (Cadi et al., 2004). However, in other European localities, such as central Italy, the viability of reproduction has been questioned (Luiselli et al., 1997).

Clutch number

Constraints of abdominal cavity influence clutch size in chelonians, but females may increase their annual fecundity by producing multiple clutches per year (Moll, 1979; Congdon and Gibbons, 1985). Species with longer nesting seasons increase the possibility of laying more clutches in relation to other species having a shorter nesting period. Species laying multiple clutches have longer reproductive periods than species laying a unique annual clutch (Moll, 1979). Female Trachemys venusta lay up to six clutches in Panama (Moll and Legler, 1971) and four clutches in Mexico (Vogt, 1990), in nesting seasons of 4–5 months. North American female T. s. elegans may lay at least three different clutches annually, with internesting periods of 14–22.5 days (Tucker, 2001). Although information on successive clutches from females in southern Spain was not obtained, the number of different groups of follicles and eggs suggest that at least up to four clutches annually may be produced. Considering the internesting interval described for this subspecies, a maximum number of five to eight clutches could be expected in the four months of the nesting season in this area.

Fertility rates

In a newly established population, the sex ratio could be unequal, and the number of available males may be insufficient to fertilize all clutches. However, although the proportion of males in relation to females was found to be low in one of the two populations studied (Perez-Santigosa et al., 2006a), fertility rates were high, and all clutches inspected had fertile eggs. The low proportion of males could be compensated for by sperm storage, which has been reported to occur in this species (Gist and Congdon, 1998). Fertility rates were even higher in clutches of T. s. elegans than in native aquatic turtle species, which may also use stored sperm; however, fertility in native clutches fertilized by stored sperm has been reported to decrease (Roques et al., 2006).

Comparison with native turtles and implications for conservation

Trachemys s. elegans is considered at present to be among the 100 most invasive species in the world (Lowe et al., 2000). Low population increase and moderate reproduction characteristic of chelonians imply that this is not an explosive species capable of rapid colonization of feral habitats. Among chelonians, however, T. s. elegans is one of the species with earliest maturity and greater fecundity than most other species, which favour population establishment in new habitats. In competition with native chelonians, invasive T. s. elegans could reach a larger number of individuals in optimal environments, with favourable availability of resources. In comparison with native aquatic turtles from the localities studied in southern Spain (M. leprosa and E. orbicularis), exotic turtles reach maturity at an earlier age, are more fecund and fertile (Table 3), and would be favoured by their larger body size in agonistic encounters for resources. In fact, T. s. elegans has been reported to affect survival of E. orbicularis, competing for basking sites (Cadi and Joly, 2004) while the displacement of individuals of M. leprosa has also been detected in the study areas (unpublished data). Thus, the

Table 3. Comparison of the main reproductive characteristics of Trachemys scripta elegans and of the two native aquatic turtles from southern Spain

	Trachemys s. elegans	Mauremys leprosa	Emys orbicularis
Female SCL (mm)	211.0 (170.7–257.85)	176 (131.5– 228)[a]	142.6 (129–167)[a]
Female mass (g)	1408.4 (718–2700)	743.7 (329–1650)[a]	526.6 (340–820)[a]
Nesting season	April–July	May–June[a]	June–July[b]
Clutch number	>=4	2[a]	2–3[a]
Clutch size	11.5 (6–16)	6.4 (3–13)[a]	6.4 (3–10)[a]
Age at maturity (years)	3–4–5	7[a]	Approx. 5[e]
Size at maturity (mm)	170–171	120–140[a,d]	129.8[a]
Fertility	79.5%	78.27%[c]	76.44%[b]

[a] Keller (1997).
[b] Roques et al. (2006).
[c] Authors' unpublished data based on incubation of 76 eggs (from 14 clutches) at constant 28ºC.
[d] Perez et al. (1979).
[e] Estimated from the age of females calculated in relation to the size (SCL) at maturity, after Keller (1997).

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introduction of this exotic species constitutes a major threat to the conservation of these two native species.

Programmes of capture and removal of exotic species are at present being carried out in southern Spain. Knowledge of the reproductive characteristics of T. s. elegans provides basic, relevant information with which to improve programmes of eradication, which should be continued for a period of 3–5 years after removal of adults, to prevent re- establishment of the population due to maturation of unobserved juveniles or hatching of undetected eggs. The search for females around their aquatic habitats during the long nesting period, from April to July, when they may be captured easily by hand, is also worthwhile in these programmes. Extraction of females and detection of their nests effectively decrease the annual reproductive output of feral populations. Other actions needed to complement these programmes are to reduce, or even to prohibit massive importation of turtles for the pet trade, and to avoid the release of pets in the wild by means of public education initiatives.

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